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POLLINATION OF ORCHIDS THROUGH PSEUDOCOPULATION

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WITHIN comparatively recent years, biologists have been made aware of a peculiar relationship between certain orchids and the hymenopterous insects which pollinate them. A wholly unexpected trend in biological behavior has been revealed and it has been proved that the motives leading to pollination are much more complex than formerly had been supposed. It is now known that certain insects are attracted by orchids for a purpose wholly apart from the search for food and that there are aspects of pollination presenting new and practically unexplored fields for research.

The historical approach to the subject of the pollination of orchids carries us back to what may be termed the beginning of the rational epoch in natural history, when guess-work and philosophical speculation were steadily giving ground to critical studies and reasoned research. Indeed, it was the mystery surrounding the methods of fecundation in the Orchidaceae that impelled Robert Brown to review the theories that had been propounded from 1760 down to 1831 and to examine the matter by actual observation. In the Transactions of the Linnaean Society for 1833 appeared Brown's famous

paper "On the Organs and Mode of Fecundation in Orchideae and Asclepiadeae" (Trans. Linn. Soc. 16 (1833) 685-733), and it was through his critical investigations of the tissues of orchids in the furtherance of his knowledge of this subject that he noticed for the first time the nucleus of the cell and in defining it, hit on the exact term which later became adopted in the vocabulary of science.

It is interesting to learn, from Brown's remarks, of the obscurity that once surrounded what is today so obviously and so definitely implied by the sexual apparatus of the most simple species. There were two schools of thought regarding the methods of fecundation in the orchids: one claiming that direct application of the pollen to the stigmas is necessary to bring about fecundation; the other regarding direct contact between pollen and stigmas too difficult of accomplishment or altogether improbable, and the proponents of this idea suggested other means than direct contact between pollen and stigmas by which the fecundating material reached the ovules. Brown concluded that the application of pollen to the stigmas is the only way in which impregnation of the ovules is effected, and referred to J. K. Wächter who was the first man to demonstrate experimentally that pollen must reach the stigmas if fertile seeds are to be produced and that if insects are excluded from the flowers fertile seeds fail to develop. This was in 1801.[1]

In 1862, before the Linnaean Society of London,

[1] "Ich zog nämlich Orchis bifolia in der Stube in Topfe, und hielt, so viel wie möglich, Insecten und äussere Zufälle von den Blumen entfernt. Jede Anthere blieb in ihrer häutigen Einlassung verschlossen, dagegen nahm ich bey einigen Blumen die Antheren mit einer Pincette heraus, und befruchtete die Narbe. Nur bey diesen schwoll nach einiger Zeit das Germen auf, und trug eine grosse Menge Saamen; – alle übrigen blieben unfruchtbar." J. K. Wächter, Römer Archiv für die Botanik 2, (1801) 209.

Charles Darwin read a remarkable paper on the sexual forms of Catasetum, a genus of the Orchidaceae characterized by extraordinary dimorphism. In the same year his classic treatise on the relation between insects and orchids appeared. This comprehensive work, spiced with conjecture, gave the results of patient observation and not only banished all doubt regarding the function of the pollinia, but centered the attention of naturalists on the complex symbiosis existing between orchids and food-seeking insects. Since Darwin's treatise on orchid-pollination was published, there have been many contributions to the subject, but these have been scattered in various journals and have to do for the most part with single species.

One would be justified in concluding that the examples of pollination as Darwin described them for Catasetum and Coryanthes constitute the most complicated symbiotic relationships to be found in the orchid family; but the recent discoveries made by Pouyanne, Godfery and Mrs. Edith Coleman have revealed equally complicated relationships and have indicated the necessity for close scrutiny of the behavior of insects that pollinate orchids.

In February 1916, in the Journal de la Société Nationale d'Horticulture de France there appeared the first of a series of articles contributed by Monsieur A. Pouyanne and submitted to the Society by Monsieur Henry Correvon. Pouyanne, during his long residence in Algeria where he served as President of the tribunal of Sidi-Bel-Abbès, had observed the pollination of several species of Ophrys and had arrived at truly startling conclusions; indeed, he had arrived at conclusions so startling that painstaking confirmation, carried on through twenty years, preceded their publication.

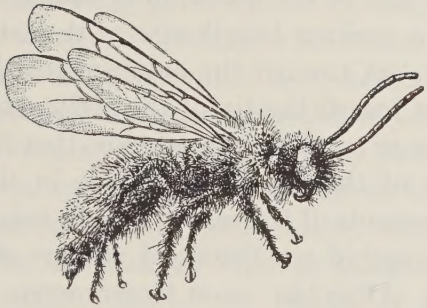
Pouyanne observed pollination in *Ophrys speculum*

Link, *O. fusca* Link and *O. lutea* Cavan. He learned that the flowers of *Ophrys speculum* are visited not only by a single species of insect, *Scolia (Dielis) ciliata* (Fabr.),[2] but solely by the males. The females exhibited complete indifference to the orchid although visiting the flowers of species of Centaurea, Galactites, Malva and Reseda in search of food. Both sexes visit species of these genera and both the males and females then use the proboscis in sipping nectar.

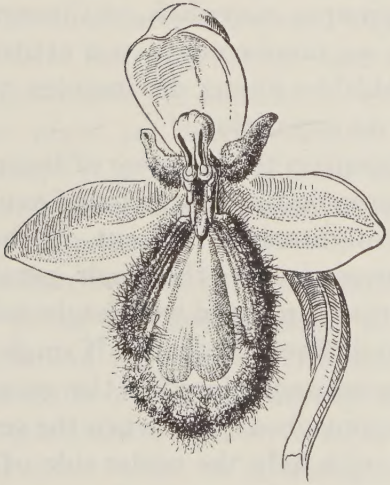
Scolia ciliata is a member of the Scoliidae, a family of burrowing hymenoptera, whose burrows are made in sand-banks exposed to the sun. The males emerge from the burrows about a month earlier than the females, usually in March. The females lead an almost subterranean existence and leave the burrows chiefly in search of food. While waiting for the females to make their appearance (mating takes place only in the open air), the males may be seen exploring in sinuous flight the ramparts of Algerian fortifications and exposed railroad embankments. And it is just such places as these for which the plants of *Ophrys speculum* exhibit a predilection. The flowering season of the orchid coincides with the appearance of the males of *Scolia ciliata* and during the long wait for the coming of the females, the male insects visit the orchid flowers, seeming to find in them a compelling attraction. There were questions here demanding deep thought. In the first place, why the indifference of the females? And in the second place, what attributes peculiar to *Ophrys speculum* were of a nature to attract one sex and not the other of an insect seeking food?

Pouyanne established beyond any doubt that the flowers of *Ophrys speculum* are not visited for nectar or

[2]Pouyanne referred to this insect as *Colpa aurea*. In more recent accounts the name *Dielis ciliata* Fabr. has been used. In this paper I have adopted the view that Dielis is a subgenus under Scolia.



1. Scolia (Dielis) ciliata *(Fabr.)*
A male, three times natural size.



2. Ophrys speculum *Link.*
A flower, three times natural size.

edible tissues, because when the males of *Scolia ciliata* enter a flower the suctorial apparatus is not used and the proboscis of the insect does not come in sustained contact with any part of the labellum of the orchid. The insect assumes a position lengthwise of the labellum with the head directed toward the column, just beneath the rostellum, and inserts the tip of the abdomen among the reddish yellow or maroon colored hairs that form a fringe near the apex of the labellum. While in this position, peculiar movements of the insect's body take place; the pollinia of the orchid are dislodged and are affixed to the insect's head. After the usual hygrometric behavior of the pollinia the pollen masses are in a position for coming in contact with the stigmas of the next flower visited. Pouyanne observed the action of the insect after the tip of the abdomen had been inserted among the hairs of the labellum and described it as follows: "Le bout de l'abdomen est alors agité, contre ces poils, de mouvements désordonnés, presque convulsifs, et l'insecte tout entier se trémousse; ses mouvements, son attitude paraissent tout à fait semblables à ceux des insectes qui pratiquent des tentatives de copulation."

Seeking to explain the behavior of the males of *Scolia ciliata*, Pouyanne conducted a series of experiments that might prove enlightening. He cut off the labellum of some of the flowers, leaving the sepals, petals and column intact. Flowers so mutilated were neglected; the insects became quite indifferent to them. If single flowers were taken from a raceme and placed on the ground, they were immediately approached. But when the separate flowers were inverted with only the under side of the labellum exposed, the insects still came to them, yet with lessened interest. If a bouquet of flowers was held in the hand, the males of *Scolia ciliata* came to it in numbers, contending with each other for the possession of a labellum. If,

however, such a bouquet was forced on the attention of the females, they exhibited indifference, and if pressed too insistently flew away as if from something repugnant to them. If flowering specimens of the orchid were concealed under sheets of newspaper and thus hidden from view, the males of Scolia would approach, as if trying to reach the concealed flowers, attracted, it would seem, by some odor too faint for perception by human nostrils, because *Ophrys speculum* is described as being without scent. Pouyanne refers to the metallic, violet-blue patch of color on the labellum of *Ophrys speculum* as resembling the metallic blue of the female of *Scolia ciliata* when, at such times as the insect is at rest or crawling on the ground, the wings are half crossed. It is then that the insect, if the sun is shining, exhibits a metallic lustre, an iridescence, similar to that of the labellum of *Ophrys speculum.* Even though the resemblance between the female of *Scolia ciliata* and the labellum of the orchid is hardly of a nature to deceive our eyes, Pouyanne reminds us that the vision of insects is myopic and less keen than ours and that, moreover, in addition to even a faint resemblance that might not in itself deceive the males of *Scolia ciliata,* there is some subtle scent that completes the deception and induces the sexual phenomena he has so convincingly described.

From Pouyanne's experiments and from the behavior of the insects there was every reason to believe that *Ophrys speculum* and the males of *Scolia ciliata* are biologically adjusted for purposes mutually advantageous, although if the purposes are purely sexual, as is evident, then the orchid alone seems to be biologically benefited by the association and, according to human standards, the insect seems to be sadly hoodwinked.

We may wonder how the brief time between the emerging of the males and the females of *Scolia ciliata,*

about thirty days each year, was turned by the plant through the ages to such advantage to itself, because in seasons when the orchids are late in flowering or the females of *Scolia ciliata* emerge from their burrows earlier than usual, the orchids are neglected and yield few if any seeds. And once the females of *Scolia ciliata* appear, the males apparently lose interest in the orchid-flower and pseudocopulation is no longer performed. Here indeed is a circumstance that is rather amazing. It forces us to assume gradual change and a series of slow modifications through a prodigiously long period of time before the male insect and the orchid became biologically adjusted. Is it not true, that in contemplating the action of Natural Selection as Darwin propounded the doctrine, we think of modifying influences as being prolonged or in constant operation on the affected organism? And yet the direct stimuli associated with pseudocopulation that have affected the flowers in the case of *Ophrys speculum*, have been confined in their action to the brief flowering period, to the duration of anthesis, and under certain circumstances, in exceptional seasons, may operate for a very limited time.

After studying the relationship between *Ophrys speculum* and *Scolia ciliata* it would seem that the marvels of orchid-insect symbiosis had reached the furthermost limit of specialization, but such is not the case, because the observations of Monsieur Pouyanne in Algeria and of Colonel M. J. Godfery at Hyères in the south of France, on other species of Ophrys, and the observations made by Mrs. Edith Coleman in Australia with regard to the pollination of *Cryptostylis leptochila*, through symbiotic relations with an ichneumonid wasp, throw the whole matter of sexual relationship between orchids and insects into the realm of fascinating conjecture and stimulate the belief that in some departments of orchidology we are

simply at the threshold of enlightening investigation.[3]

As in other fields of human experience, so in biology, it seems that unusual discoveries are announced almost simultaneously. Pouyanne may have formed very definite conclusions regarding *Ophrys speculum* many years before he published the results of his observations in 1916, but the first reference to this symbiotic phenomenon was followed in 1925 and in 1927 by the announcements of the independent observations of Godfery in France and of Mrs. Coleman in Australia.

Usually when we describe the pollination of orchids by insects we explain that the pollinia become attached to the insect's proboscis, head or thorax and that this is so because the insect enters the flower head foremost and eventually comes in contact with the rostellum, that extraordinary third stigma, or female organ, modified to serve as an efficient means of attachment of the pollinia to the insect. But this is not always so. There are cases,

[3]Robert Brown was of the opinion that the flowers of *Ophrys apifera* resemble bees to repel, not to attract, insects. Darwin in a footnote in his treatise, On the various Contrivances by which British and Foreign Orchids are fertilised by Insects, has the following: "Mr. Gerard E. Smith, in his Catalogue of Plants of S. Kent, 1829, p. 25, says: 'Mr. Price has frequently witnessed attacks made upon the Bee Orchis by a bee, similar to those troublesome Apis muscorum.' What this sentence means I cannot conjecture." It is possible that we have here the first reference to pseudocopulation between insects and orchids.

In the Journal of Botany (68 (1930) 280-281) H. G. Willis directs attention to pollination in the Fly Orchis *(Ophrys muscifera)*, stating that he saw a fly visit this species in 1877 and that a few years later an account of his observations was published in the Transactions of the Manchester Microscopical Society reporting him as having said, "To me at the time it seemed obvious that the male fly came to the flower mistaking it for a female." Godfery has observed pollination in this species effected by the males of *Gorytes mystaceus* L., the insects behaving in a manner that suggested a preliminary phase of courtship. (Journ. Bot. 67 (1929) 299).

rare indeed, when the insect inserts its *abdomen* between the rostellum and the base of the labellum and removes the pollinia on the posterior part of the body. If this occurrence proved to be strictly localized, we might accept it without too much concern; but when we find that it is not localized but takes place in the Mediterranean region and also in Australia, it becomes a matter fraught with fascinating biological significance.

In *Ophrys speculum* the labellum resembles an insect with its head facing the column and when *Scolia ciliata* enters the flower it does so head foremost. But in *Ophrys lutea*, a species observed by Pouyanne in Algeria, the labellum has in its centre certain markings that he described as being similar to the female of an insect with its head directed toward the apex of the labellum. When the males of species of Andrena visit the flowers (and here indifference on the part of the females is again to be noted), they assume what may be termed a reverse position, the abdomen being directed toward the column, the head toward the apex of the labellum. The insect inserts the tip of the abdomen in the cavity at the base of the labellum and after executing movements suggesting sexual excitement, departs bearing the pollinia *on the tip of the abdomen*. The same phenomenon has been reported for *Ophrys fusca* by Pouyanne, and by Godfery who observed insects visiting this orchid in the garden of the Hôtel Continental at Hyères. Godfery also observed *Andrena trimmerana* Kirby visiting *Ophrys arachnitiformis* Gren. & Phil. at Hyères. In this case the insect removed the pollinia on its head, but when it visited *Ophrys fusca* it carried the pollinia on the tip of the abdomen, having assumed the reverse position on entering the flower. As a result of the observations of Pouyanne and Godfery, it is apparent that *Ophrys speculum* is visited only by the males of *Scolia ciliata* which remove the pol-

3. Andrena nigroaenea *Kirby*
A male, three times natural size.

4. Andrena trimmerana *Kirby*
A male, about three times natural size.

5. Ophrys fusca *Link.*
A flower, three times natural size.

linia on the head; *Ophrys lutea* is visited by the males of *Andrena nigro-olivacea* Dours and *Andrena senecionis* Perez, and *Ophrys fusca* only by the males of *Andrena trimmerana* Kirby and *Andrena nigroaenea* var. *nigro-sericea* Dours, all of these insects entering the flower in the reverse position and removing the pollinia on the tip of the abdomen.

In Australia, in May 1927, Mrs. Coleman published a preliminary statement, in the Victorian Naturalist, describing the behavior of the Ichneumonid wasp *Lissopimpla semipunctata* Kirby which visits the orchid *Cryptostylis leptochila* F. v. Muell., but she refrained at that time from giving free expression to the conclusions she must have drawn, and simply stated two facts: that the insect visits the orchid and assumes the reverse position; that the insect effects pollination. In the following year (April 1928), Mrs. Coleman published a second paper in the Victorian Naturalist, giving a detailed account of further observations on *Cryptostylis leptochila.* Her conclusions were so extraordinary that they would have justified incredulity had not the opinions of other investigators substantiated them. She linked the Australian case with the ones observed in Algeria and France. There was no doubt in her mind but that the orchid flower, through what she termed mimicry, exercises sexual attraction for the males of *Lissopimpla semipunctata* and she assumed that mimicry of form is reinforced by a scent too faint for perception by human beings.

Besides the lure of "mimicry" it is indeed highly probable that the orchid gives off a scent that produces a stimulus at a distance because the flowers, even when taken into a room with partially closed windows, are visited by the males of *Lissopimpla semipunctata.* On one occasion when flowers were placed on a shelf beneath a window they were visited almost instantly by three

males, surely evidence that scent plays a part in this remarkable relationship between orchid and insect, notwithstanding the reports that *Cryptostylis leptochila* is odorless or emits only a faintly perceptible odor.

After studying such subtle modifications, we are reminded of Darwin's words: "Unless the flowers [of orchids] were by some means rendered attractive, they would be cursed with perpetual sterility."

A glance at the strange labellum of this Cryptostylis, modified out of all proportion to the almost thread-like sepals and petals, with its double row of dark glistening glands that gleam in the hot sunshine loved by the wasp, is perhaps sufficient to justify the theory of an attraction based on the resemblance of the flower to a female Lissopimpla. The male wasp always assumes the reverse position with the head facing the apex of the strongly sigmoid labellum. It opens the tip of the abdomen, apparently fastens the claspers to the fleshy folds of the labellum at the base and thrusts the aedoeagus into the stigma, when seminal fluid is ejected. In the meantime the tip of the abdomen has been pressed against the viscid disc of the rostellum and when the insect departs it carries the pollinia fastened to the posterior part of the abdomen. Tarlton Rayment in his recent book "A Cluster of Bees" gives a brief description of this phenomenon and thus lends the weight of his entomological knowledge to the conclusions at which Mrs. Coleman arrived.

One might be led to expect that *Cryptostylis leptochila*, through its association with *Lissopimpla semipunctata*, would exhibit a distribution similar to that exhibited by the insect. But this is not so. Lissopimpla is found in all the Australian States and also in New Zealand, while *Cryptostylis leptochila* is confined to Victoria and New South Wales, its capacity for spreading being limited by those factors that govern endemism. Yet if the orchid

is taken to localities beyond its natural range, the males of *Lissopimpla semipunctata* will visit the flowers and behave toward them in the manner described above. It is now known that *Lissopimpla semipunctata* does not confine its attentions to *Cryptostylis leptochila*, but pseudocopulates with three other Australian species of the genus: *C. subulata* Reichb. f., *C. erecta* R. Br. and *C. ovata* R. Br.[4] possessing as it were an orchidaceous harem.

While Ophrys is essentially a European group with a few outlying representatives in western Asia and northern Africa, and includes approximately twenty-nine species, Cryptostylis extends from India to the South Sea Islands and comprises about thirty species. Cryptostylis is one of two genera referred by Rudolf Schlechter to the Cryptostylideae, a subtribe rather sharply set apart from its generic allies. This taxonomic isolation of Cryptostylis is significant when regarded in the light of Mrs. Coleman's observations. Its wide distribution in the tropics stimulates the expectation that when further studies are made of the methods by which the other species are pollinated, new and equally startling relationships may be revealed.

Since 1916 when Pouyanne's observations were published, pseudocopulation has been recorded for at least six species of Ophrys and for four species of Cryptostylis. As Ophrys and Cryptostylis belong respectively to two of the basic subdivisions of the monandrous orchids and are widely separated, each the product of a distinct line of descent, it is evident that pseudocopulation was either a primitive development in the Orchidaceae or originated

[4]Mrs. Coleman has described the visits of an insect to another Australian orchid, a species of Caladenia, and implies that pseudocopulation is performed, although as yet the identity of the insect has not been established and the actual removal of pollinia has not been observed. The Victorian Naturalist 46 (1930) 203-206.

independently more than once as a symbiotic phenomenon; not only independently with regard to the phylogenetic position of the genera affected, but with regard to the geographical distribution of those genera. The assumption that pseudocopulation has had an independent origin phylogenetically and geographically, arouses the thought that there is perhaps some prevalent attribute of the Orchidaceae, aside from any morphological character, that permeates the species and underlies orchid-insect symbiosis.

It is illuminating to examine the evolutionary significance of pseudocopulation in the light of taxonomic evidence because, of the forty-five genera constituting the Basitonae or Ophrydean orchids, Ophrys is regarded as being the most primitive genus, while, of the three hundred and sixty or more genera constituting the Acrotonae, Cryptostylis is ranked as being the thirtieth genus. Allowing for differences of opinion, and in this case they are delightfully negligible, the positions assigned to Ophrys and Cryptostylis indicate that pseudocopulation, no matter what future studies and discoveries may reveal with regard to its occurrence, is a peculiarity of the lowest groups of the orchid family and therefore may be considered an ancient and long established association. For this supposition one might expect to find helpful evidence in the paleobotanical record, but there are not any fossil orchids, notwithstanding Massalongo's Protorchis and Palaeorchis from the Eocene of Monte Bolca. Although these may be regarded as being Monocotyledons, they are wholly doubtful orchid concepts. The orchids, probably as a result of sparse distribution, appear either to have eluded the processes of fossilization or to have escaped detection. As for the insects known to be associated with pseudocopulation, none of the species has been recorded in the fossil state although the genus Andrena

is very ancient and is represented in Baltic amber. However, in appraising the value of the evidence supplied by fossils with regard to the antiquity of particular genera and species, we have to urge caution regarding the significance of negative evidence because fossils in museum collections constitute a pitifully incomplete record of the past.

From the known examples of orchid-insect symbiosis it becomes clear that orchids have derived profit from two of the dynamic urges of animals: *hunger and sex.* In Coryanthes and Catasetum the pollinating insects seek food. The flowers of these genera have developed edible tissues that attract certain bees, and in the course of evolution their floral structures have become so modified that food-seeking bees bring about pollination. In Ophrys, on the other hand, where nectar is wanting, and in several of the better understood members of this genus which seem to lack edible tissues, it is not the urge of hunger that motivates the insects necessary to effect pollination, but the equally dominant sex-impulse. Probably in the course of evolution, these orchids gradually lost the capacity to produce nectar or edible tissues and by some passive response to stimuli incident to the dynamic sexual urge of certain insect-visitors became so modified in structure that they seem to simulate the female of a particular insect species. In this connection it is difficult to escape the conclusion that such orchids as *Ophrys speculum*, by "mimicking" the female, in becoming by evolution dependent for pollination on the male of a single species of insect, have been marvellously even if perilously specialized.[5] In the final analysis there is something

[5] *Ophrys speculum* is a widely distributed species in the Mediterranean region and it is not at all improbable but that as its pollination history becomes better known we may find other insects associated with the transportation of the pollinia.

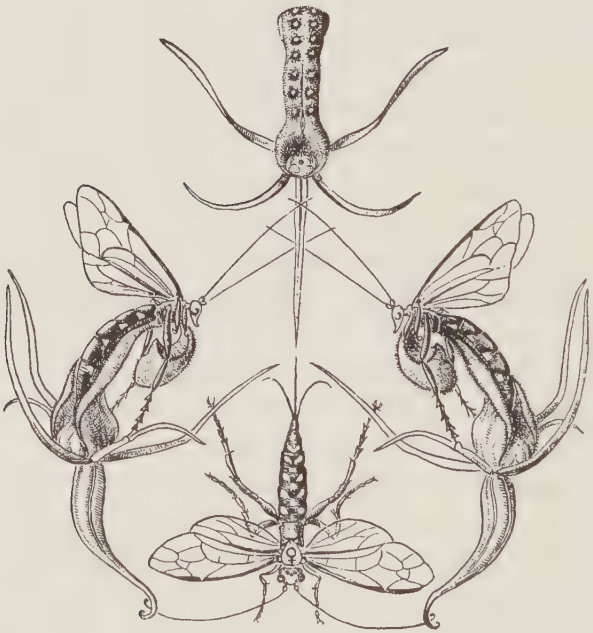
definitely awe-inspiring in the pollination-history of the orchids when it is understood that to ensure their sexual success there has been developed subserviency to two of the dominating instincts of animals: *the urge of hunger and the sexual impulse.*

Before us is a teasing question. It arouses keen curiosity and stimulates the wish to know more than we do about the actual history of biological change, not only as it relates to the origin of species but to the actual shaping of flowers. Perhaps it is easy to visualize gradual change in form where structures are supposed to be continually responding to environmental influences until complexity replaces simplicity, but when into the theatre of our imagination we usher such organisms as *Ophrys speculum* and *Scolia ciliata* and command them to play out their evolutionary story and exhibit how the duration of anthesis has been long enough to bring about the phenomena we have witnessed, it must always be in the dim light of limited understanding.

Biology is the study of protoplasmic manifestations whether these occur in structure or in behavior. Man being the only animal trying to explain itself and to ascertain the laws of destiny, tries to explain everything else. After asking pertinent questions about the obscure forces responsible for the wonderfully close association between the Ichneumonid wasp and Cryptostylis, Tarlton Rayment answered: "Who knows?" And that I fear will be the answer despite our present knowledge of tropisms and the play of hormones, even should more venturesome naturalists endeavor to plumb the depths of the pseudocopulation mystery.

It may be that those who would reject the evolutionary approach to an understanding of life and who prefer to regard the world as the product of Special Creation will lean a little more lightly on human weakness when

they discover moral turpitude among the insects. And it may be that entomologists, who see for insect societies parallels in human institutions, will become Freudian in their outlook when discussing the sexual vagaries revealed by symbiotic phenomena and introduce such terms as *Lissopimplan behavior* or *Ophrydean complex*. Perhaps even the poet will have to reconsider whether "Only man is vile."



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EXPLANATION OF THE ILLUSTRATIONS

1. Scolia (Dielis) ciliata *(Fabr.)*. A male. The insect is enlarged approximately three times natural size. The body of the insect is black with bristle-like, light brown or yellowish hairs on the thorax, abdomen and legs.

Drawn from a specimen preserved in the Museum of Comparative Zoology, Harvard University.

2. Ophrys speculum *Link*. A single flower enlarged approximately three times natural size. Sir J. D. Hooker (Botanical Magazine t. 5844) referred to the labellum of *Ophrys speculum* as follows: "the brilliant polished surface of the disc of the lip, which shines like a blue-steel looking-glass, edged with gold, and that again set in a rich maroon velvety frame, presenting a combination of colours quite unlike anything else known to me in the vegetable kingdom."

The relative lengths of the body of *Scolia ciliata* and of the labellum of *Ophrys speculum* appear to be so nicely adjusted that the insect's head comes directly under the rostellum of the flower when the tip of the abdomen is thrust among the hairs near the apex of the large middle-lobe. In this regard, and as a product of Natural Selection, the labellum of the orchid is a most interesting structure, because the marginal portion of the middle-lobe is comparatively smooth and sharply deflexed, the elongated hairs ceasing rather abruptly at the point where deflexion begins. In the illustration the marginal, smooth portion of the middle-lobe is invisible because of its being rolled downward. The rostellum (represented in the illustration by the two rounded structures at the base of the balloon-like anther situated between the two short petals) is at just the proper height (about 2 mm.) above the base of the labellum where it joins the column, to allow the insect's head to pass beneath it, but in contact with it, when the pseudocopulative attitude is assumed. There is hardly any excavation at the base of the labellum comparable to the wide-mouthed cup or depression in *Ophrys fusca* and *O. lutea*, so that the "reverse position" is not favored.

1. Scolia (Dielis) ciliata *(Fabr.)*
A male, three times natural size.

2. Ophrys speculum *Link.*
A flower, three times natural size.

3. Andrena nigroaenea *Kirby*. A male enlarged approximately three times natural size.

Drawn from a specimen preserved in the Museum of Comparative Zoology, Harvard University.

4. Andrena trimmerana *Kirby*. A male enlarged approximately three times natural size.

Drawn from a specimen preserved in the Museum of Comparative Zoology, Harvard University.

5. Ophrys fusca *Link*. A single flower enlarged approximately three times natural size. The labellum varies considerably in color, but is usually dark purple, sometimes with a narrow golden yellow border. The markings that are supposed to simulate the wings of a female Andrena (probably the partly folded wings), are lighter in color than the rest of the labellum and are more or less iridescent with greys and blues. The wing-like pattern formed by the iridescent area is in reality densely beset with minute glandular hairs, but these are so minute that to the unaided eye the surface from which they emerge appears to be quite smooth. The rest of the labellum is velvety or even hairy almost to the margin and under the microscope is sharply demarked, by the difference in the length of the hairs, from the area occupied by the iridescent wing-pattern. In some forms of this species the hairs are much elongated, as in *O. speculum*, just within the margin of the large middle-lobe. At the base of the labellum beneath the rostellum, there is a shallow cup-like depression with a broad opening. The anterior margin and wall of this depression are densely covered with short glandular hairs and the opening is sufficiently large to admit the posterior part of the abdomen of an insect that effects pollination, while the rostellum is sufficiently close to the opening to touch the posterior segments of the insect's body and to affix the pollinia in preparation for transportation to another flower.

Between *O. fusca* and *O. lutea* the differences are chiefly those to be found in the color of the labellum, the fundamental structures of the two species being very similar.

3. Andrena nigroaenea *Kirby*
A male, three times natural size.

4. Andrena trimmerana *Kirby*
A male, about three times natural size.

5. Ophrys fusca *Link.*
A flower, three times natural size.

The Australian orchid *Cryptostylis leptochila*, F.v.M. (1, 6, 9), cross-fertilised by the male Ichneumonid *Lissopimpla semipunctata*, Kirby, with which it attempts to pair (3), carrying off the pollinia (4, 5) on the end of its abdomen (2). Genitalia of male (11, 12, 13). Pollen (8); section of labellum (10); antennal segments (7).

Reproduced from a plate in the Transactions of the Entomological Society of London, 76, pt. 2, (1929) t. 24.

Drawings by Tarlton Rayment.


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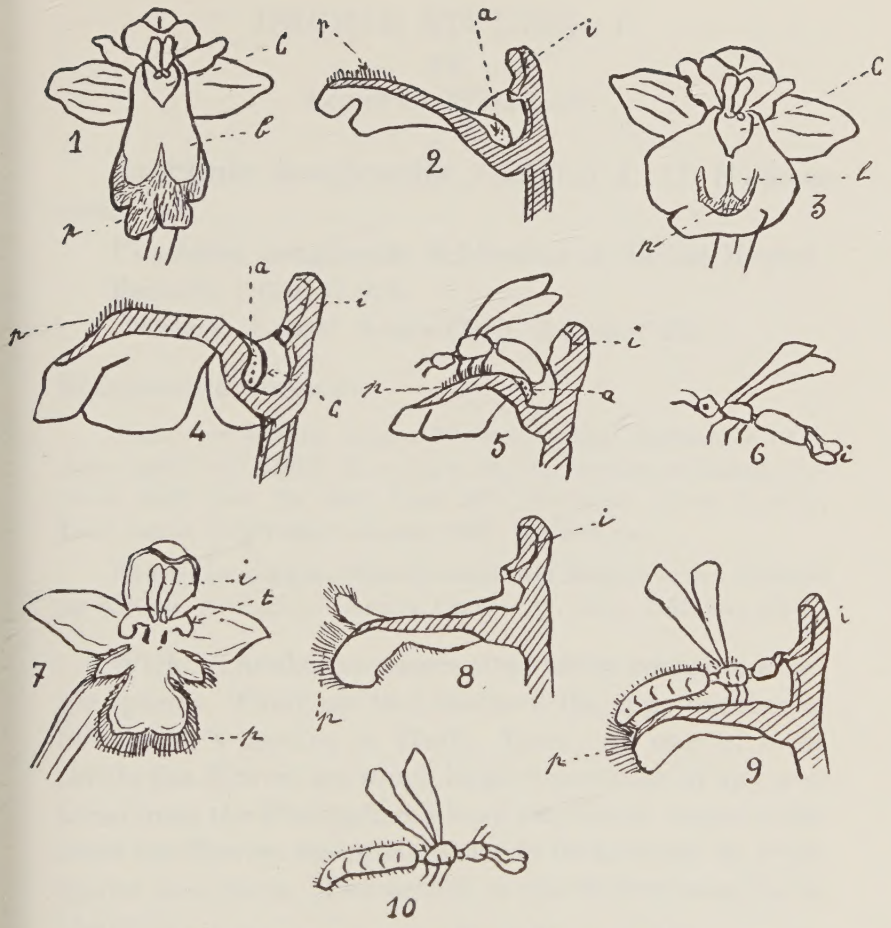

Fécondation des *Ophrys fusca, lutea et speculum.*

1, *Ophrys fusca*, fleur vue de face; 2, coupe du labelle (grossi). — 3, *O. lutea*, fleur vue de face; 4, coupe du labelle (grossi); 5, fécondation opérée par un petit hyménoptère (coupe du labelle); 6, l'hyménoptère s'envole avec les 2 pollinies fixées à l'abdomen. — 7, *O. speculum*, fleur vue de face; 8, coupe du labelle (grossi); 9, fécondation opérée par le mâle du *Colpa aurea* (coupe du labelle); 10, le *Colpa* s'envole avec les pollinies fixées sur la tête.

a, petit coussinet garni de poils courts sur lequel frotte l'abdomen de l'insecte; *b*, tache bleu métallique; *c*, cavité correspondant à l'éperon des *Orchis*, dans laquelle plonge l'abdomen de l'insecte; *i*, pollinies; *p*, pilosité fauve entourant le labelle (poils épais et longs); *t*, pétales.

Reproduced from a text-cut in Journ. de la Société Nationale d' Horticulture de France, ser. 4, 17 (1916) 45 (Cf. footnote on p. 4).

Drawings by A. Pouyanne

ORCHID STUDIES. I.

BY
LOUIS O. WILLIAMS

Arachnis longicaulis *(Schltr.) L. O. Williams comb. nov.*

Vandopsis longicaulis Schlechter in Fedde Repert. Beihefte 1 (1914) 973.

Arachnis Lyonii Ames Orch. 5 (1915) 221.

Specimens examined:

PHILIPPINE ISLANDS, Luzon, Province of Rizal. September 1909. *Loher 14583* and *14680*. Growing in rocks; Province of Isabela. Altitude 3000 feet. No date. *Lyon 126*: Mindanao. Camp Keithly, Lake Lanao. September-October 1906. *Clemens s.n.*

NEW GUINEA, Kaiser-Wilhelmsland. Auf Bäumen in den Wäldern am Kenejia. Altitude 150 meters. October 17, 1908. *Schlechter 18420.*

Without doubt the names cited above comprise a single species. There are two sheets of the type number of Schlechter's species in Herb. Ames; on one of these sheets the flowers are much larger than those of any material from the Philippines I have examined; on the other sheet the flowers are equal in size to those borne by Philippine specimens. The details of the flowers seem to be identical.

Renanthera philippinensis *(Ames & Quis.) L. O. Williams comb. nov.*

Renanthera Storiei Reichb. f. var. *philippinensis* Ames & Quisumbing in Philipp. Journ. Sci. 47 (1932) 210, t. 3, figs. 1-2; t. 7, figs. 12-19; t. 24 in part.

There is no doubt but that *Renanthera philippinensis* is quite distinct from *Renanthera Storiei* Reichb. f. Ames and Quisumbing pointed out in the original description of *R. Storiei* var. *philippinensis* that the type of their va-

rietal concept "differs radically from the species in its small stature, small leaves and flowers, and the narrower broadly truncated lateral lobes of the labellum." In addition to the differences emphasized by Ames and Quisumbing there is another difference found in the attachment and in the form of the mid-lobe of the lip. Also the two primary calli on the lip are slightly different from what obtains in *R. Storiei.*

Ames and Quisumbing gave as a reason for assigning this material to varietal rank their belief that a specimen in Herb. Ames *(Loher 6000)* constituted an intergrading form "clearly referable to var. *philippinensis.*" There are in Herb. Ames two sheets of this Loher collection. One sheet bears the terminal portion of the stem accompanied by leaves and an immature inflorescence; the other sheet bears an inflorescence with the flowers fully developed and in size equal to the flowers of *R. Storiei.* Dissections from both sheets reveal the floral structure of *R. Storiei* and differ markedly from *R. philippinensis.*

Sarcochilus Hubbardianus *L. O. Williams nom. nov.*

Thrixspermum philippinense Ames in Philipp. Journ. Sci. 8 (1913) 437.

Sarcochilus philippinensis Ames Orch. 5 (1915) 215—in Merrill Enum. Philipp. Fl. Pl. (1925) 408, non Vidal 1885.

Conformity to the accepted rules of nomenclature necessitate a new name for this rather common Philippine species. It is renamed in honor of Mr. F. Tracy Hubbard who assisted in the bibliographical research undertaken in the preparation of the treatment of the Apostasiaceae and Orchidaceae in Merrill's "An Enumeration of the Philippine flowering Plants."

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